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SUBAQUEOUS VERTEBRATE FOOTMARKS FROM THE UPPER DAKOTA FORMATION (CRETACEOUS) OF KANSAS, U. S. A.

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By

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INTRODUCTION

In 1933, a reptile subaqueous trackway from the Dakota Formation, Upper Cretaceous, of central Kansas (Fig. 1) was collected and transported to the Museum of Natural History at the University of Kansas, Lawrence, Kansas. There are three published references concerning the subaqueous trackway. In a short passage, Lane (1946, p. 322–323) provided some background on the footmarks:

> "There is in the University of Kansas Museum of Vertebrate Paleontology at Lawrence a series of over 50 tracks of a large Cretaceous crocodilian, discovered by Mr. C. T. Brandhorst of Sylvan Grove, Lincoln County, Kansas, at a site a few miles southwest of that town. Dr. C. W. Hibbard and the late W. S. Long collected over fifty of these tracks from an area about 7 x 10 feet in extent. They are large sized impressions and may well have been made by an individual of *Dakotasuchus kingi*. No actual remains of the animal that made these tracks have been recovered."

Vaughn (1956) mentioned the footmarks in support of the opinion that a second specimen of *Dakotasuchus* may have come from the Dakota Formation. Finally, Lockley (1986), based on a short description and two figures,

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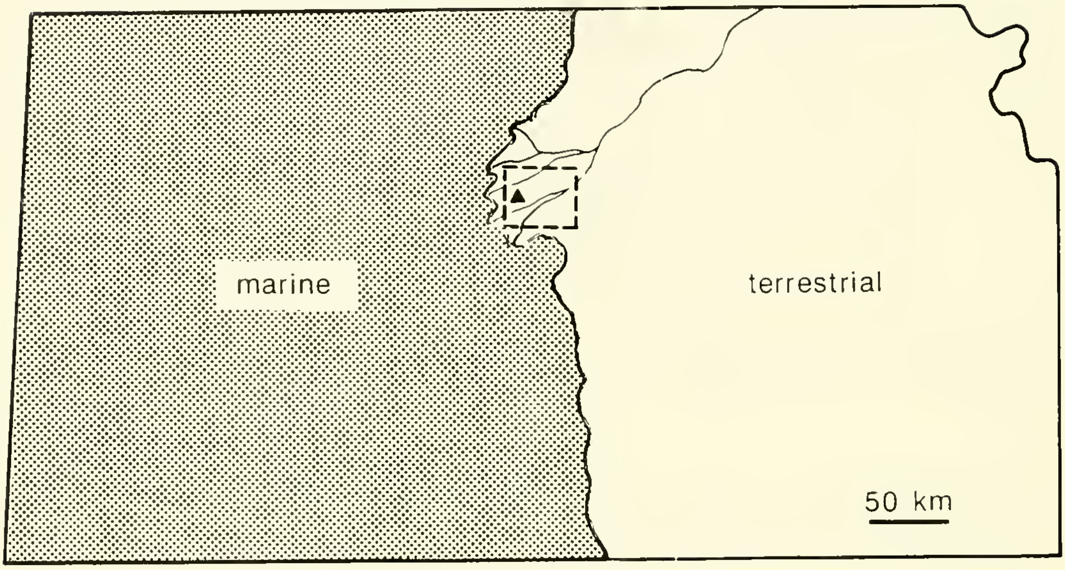

Fig. 1. Supposed paleoenvironment at one time during deposition of the Dakota Formation, Upper Cretaceous. Lincoln County in bold outline. Sylvan Grove indicated by triangle. Modified from Hattin (1967, Fig. 7).

speculates that these footmarks were produced by crocodylomorphs.

Although the footmarks have traditionally been interpreted as crocodilian, I consider this interpretation erroneous and that the probable subaqueous trackmakers were partially buoyant ornithischian dinosaurs. In addition to the new interpretation, a reassessment of the subaqueous trackways serves to document the behavior of some large reptiles in the fauna of the Dakota Formation.

The fossil record of the Kansas Dakota Formation is limited. The known vertebrate fauna includes the crocodile *Dakotasuchus kingi* (Mehl, 1941); the ankylosaur *Silvisaurus condrayi* (Eaton, 1960; Nelson, 1988); a turtle cast (Parmenter, 1899); a plesiosaur (on display at the Sternberg Memorial Museum at Ft. Hays, Kansas); and a bird track (Snow, 1885). Possibly from the Dakota Formation are four small tridactyl tracks (Mudge, 1865). Finally, there are the footmarks of at least seven individuals interpreted as ornithischians, described here. Terrestrial plants, marine invertebrates, and invertebrate trace fossils are also known from the Dakota Formation in Kansas (Hattin, 1967).

The Dakota Formation in central Kansas is between 60 and 90 m thick. It has a variable lithology consisting of shales, sandstones, siltstones and lignites and is interpreted as an alluvial plain with a north-south trending coastline (Hattin, 1967).

MATERIALS AND METHODS

The footmarks were originally impressed in mud and later covered by sand. The preservation of the footmarks is as a natural cast on the underside of the sandstone block. The sandstone of the track block is massive, non-calcareous, fine-grained well sorted arkosic material. Iron staining is present along one border of the block (the top border as viewed in Fig. 2).

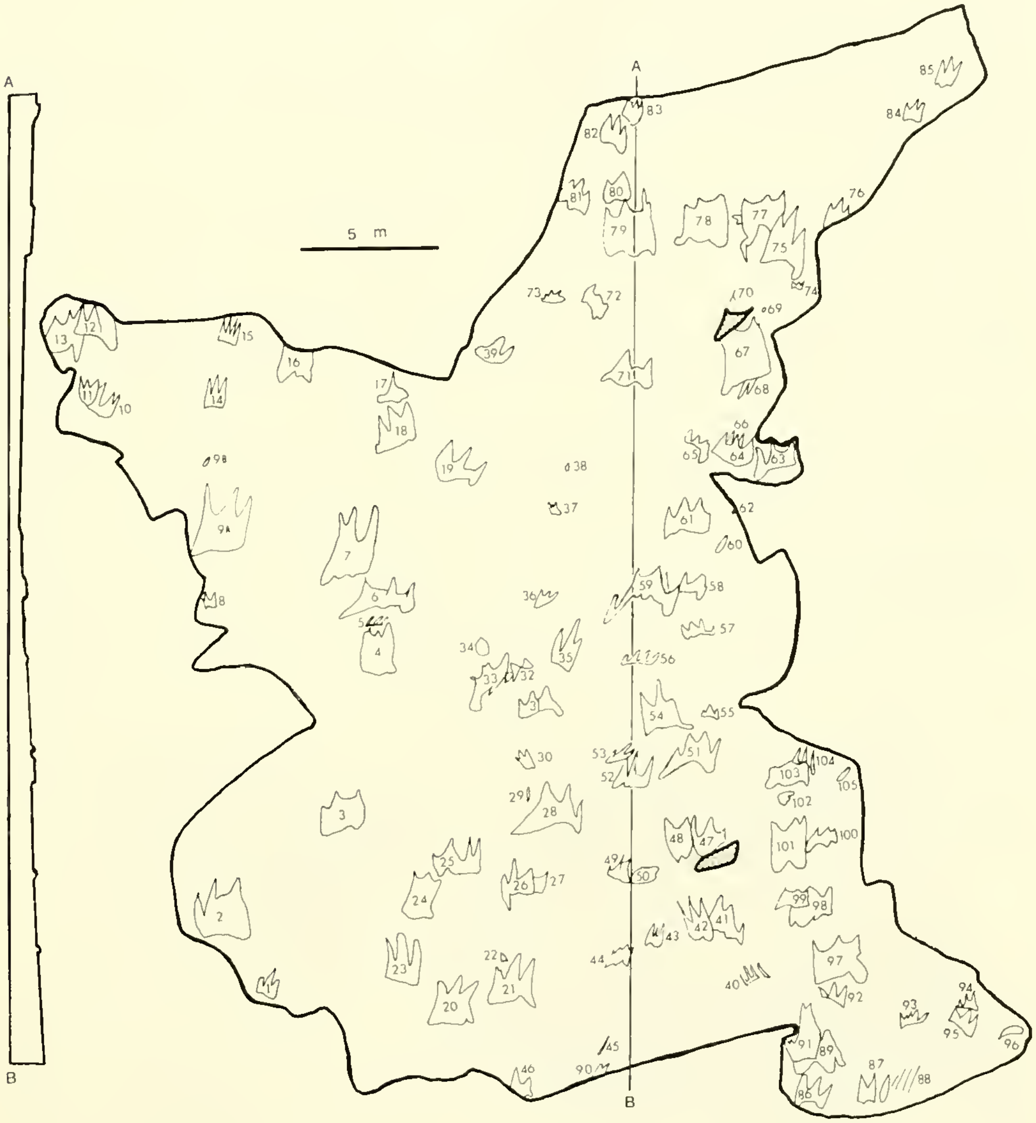

Fig. 2. Distribution of footmarks on KUVP 5914. Each mark is individually numbered. Missing portions indicated by hatched pattern. Cross-section along line AB has a depth exaggeration of 2X.

The footmarks were collected on small blocks and were transported to Lawrence, Kansas in crates. These small blocks were then assembled into the larger track block which contains 106 footmarks. Each footmark has been assigned a number (Fig. 2). There are loose footmarks that have not been assigned a place on the footmark block due to inadequate or uninterpretable field markings.

I use the width of the footmarks as a basis for size comparisons. The widths of the marks are less variable than the lengths because the makers of these footmarks could elongate their marks by extending the propulsive phase after touching the substrate.

A line was placed over the large footmark block (line AB, Fig. 2). This line has no relation to any direction but served as a reference during preparation of the subaqueous trackway block sketches, determination of orientations, and as a base line for a hypothetical cross-section.

Abbreviations used are as follows: KUVP, The University of Kansas, Museum of Natural History, Vertebrate Paleontological Collection; FHSM VP, Sternberg Memorial Museum, Vertebrate Paleontology Collection, Fort Hays, Kansas.

The terminology used throughout this description and discussion is designated as follows in order to avoid unnecessary confusion. The term trackway usually refers to a minimum sequence of three associated tracks (if the trackmaker is a quadruped then the track number is double and the sequence includes both manus and pedes in association). The term subaqueous trackway is used for the Kansas fossils as it provides a clear statement of exactly what I refer to, and it better distinguishes the inherent differences to be found in the traces produced by a subaqueous mode of locomotion (compared to more typical terrestrial vertebrate locomotory modes and their trackways). Compared to typical vertebrate trackways, subaqueous trackways do not always provide the same quality of data (and hence expectations), are not necessarily produced by similar mechanical processes (downward versus horizontal forces), or are not as readily associated into sequences of tracks (individual strides may not always leave a mark on the substrate). The scratches created by a foot will be termed footmark while the scratches created by an individual digit of the foot will be termed a digit mark.

DESCRIPTIONS

The footmarks and subaqueous trackways from the Dakota Formation of Kansas have not been described in detail nor been provided a name. Two major advantages of naming a trackway are ease of reference and the ability of the traces to avoid being 'lost' in the literature. However the advisability, and the desired degree of foot reproduction necessary for naming subaqueous trackways is controversial. Additionally, the disadvantage of naming a trackway that could easily be a modified form of another taxon (based on mode of formation) and the lack of consensus at this time of a standard framework for classification of the Kansas footmarks would justify postponing a formal name at present. Possibly a name for these footmarks may be justified in the future.

General Description—Subaqueous trackway: quadrupedal, moderately narrow pace angulation (80–125 degrees), mark of manus closer to midline than pes, tail drag absent. Manus footmark: pentadactyl but most commonly tridactyl, lateral digit marks extend posteriorly farther in footmark, width

50–60% of pes width, phalangeal trace indicates blunt short subequal digit lengths. Pes footmark: tridactyl, digit II mark often projecting posteriorly, digit marks indicate nearly equal digit lengths, distance between axes of digit marks II and III shorter than between III and IV. All footmarks: marks of phalanges and claws elongated antero-posteriorly, striated impression of phalangeal-metapodial joint present between digit marks, digits subparallel, drag marks from retraction phase present.

Locality—Three miles southwest of Sylvan Grove, Lincoln County, Kansas; Dakota Formation, Upper Cretaceous.

Described Specimen—KUVP 5914, a sandstone block containing 106 footmark casts.

Identical Footmarks—FHSM VP 138, a slab with 23 footmarks, from the same locality. A footmark similar to the Kansas manus footmarks is in the Stovall Museum collection in Norman, Oklahoma. That footmark is from Cimarron County, of Cretaceous age and is associated with fossil leaves.

Manus—A manus mark can easily be distinguished from a pes mark by its smaller size and the shape of the posterior border (compare Figs. 3A, 3B). In the manus footmark the most lateral digit mark extends farther posteriorly. The mark of digit I is smaller than the other marks of the hand. Measurements of a well defined manus mark (Fig. 3A) are presented in Table 1.

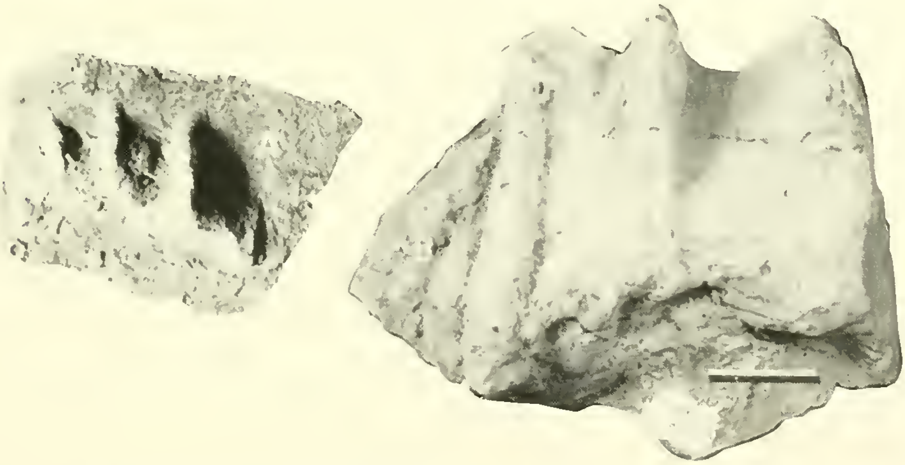

Fig. 3. Photograph of (A) right manus mark, no. 57; (B) right pes mark, no. 63. Both from KUVP 5914. Scale equals 5 cm.

The medial and lateral side of the footmark can be determined by inspection of footmarks no. 56 and no. 57 (Fig. 2). Footmark no. 56 is of a left manus which immediately preceded no. 57, a right manus, in subaqueous trackway S. The manus marks exhibit from two to five digits. In all cases the marks are of the tips of the digits.

There is a general increasing size trend in digit marks I through III and a decrease from digit mark III to IV. This likely corresponds with digit size. If digit III is longest it would strike the sediment a little farther anterior than the other digits upon initial contact. Digit mark IV is in some cases as anterior in

TABLE 1. Manus mark, based on no. 57 (Fig. 3A). Total length: 6 cm. Total Width: 11 cm. Length A: 2 cm.

Digit Mark Number	I		II		III		IV
Digit Mark Length	4.0 cm		5.5 cm		5.5 cm		3.5 cm
Interdigital Distance		3.0 cm		3.4 cm		3.8 cm	
Digit Mark Angle (in degrees)		9		13		-8	

position and as long as digit mark III.

Examination of the posterior edges of the manus marks reveals that the individual digit marks extend posteriorly farther with increasing digit number. Digit mark II extends past digit I by a small distance. Digit mark III extends past II by a larger distance, and digit mark IV extends past III by an even larger distance (Fig. 4). Based on this relationship, it is reasonable to interpret the manus marks with three digits marks to represent digits II, III, and IV. For example, in the three digit manus mark no. 55 (Fig. 4B), the posterior extension of the most lateral digit mark would seem better interpreted as digit mark IV than III. This is because the posterior extension of the lateral mark compared to the middle mark is relatively longer than the middle mark past the medial one. This relationship can be compared to the condition in no. 57 and no. 40 (Figs. 4C, 4D). Additionally, digit mark III is the most anteriorly extending as would be expected in most cases.

It is important to be aware of the general nature of traces while discussing interpretations. Trace shape is dependant not only on the shape of the manus

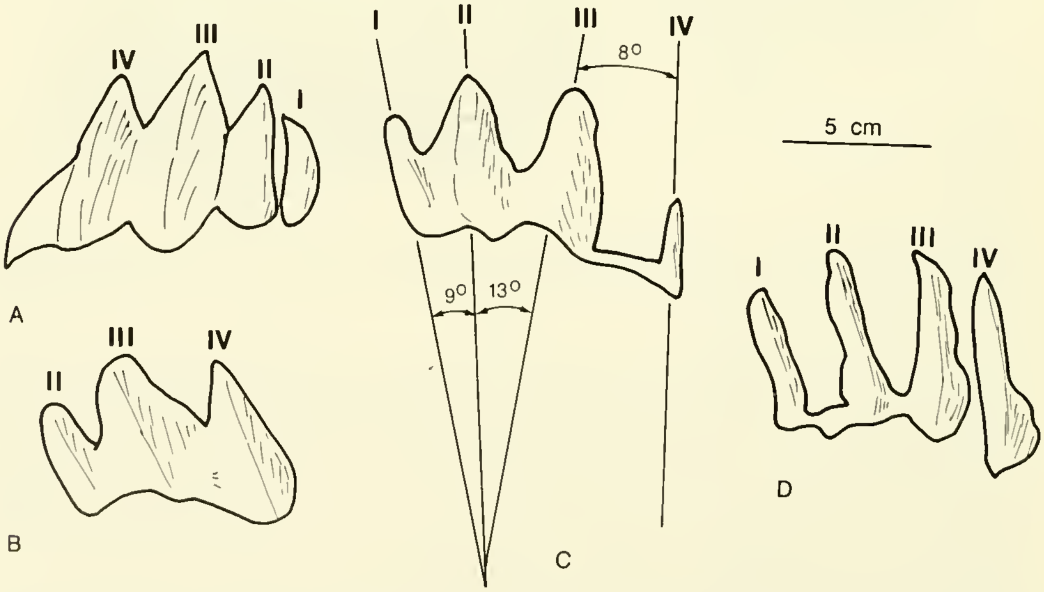

Fig. 4. Sketches of selected manus footmarks from KUVP 5914. (A) left manus mark, no. 100; (B) right manus mark, no. 55; (C) right manus mark, no. 57, with interdigital angles; (D) right manus mark, no. 40.

of the animal but the dynamics of the foot-sediment interaction. For example, digit IV was shorter than III and conflicting observations of the marks (some marks of digit IV are longer than those of III) is probably due to variation in the position of the manus during footfall.

The most force was transmitted through digit III; the digit III mark is the deepest and best preserved. Strangely, depth does not seem to correlate with the number of digits present. Of the four footmarks in Fig. 4, no. 40 (Fig. 4D) has digit I best represented and this is the most shallow of these four footmarks. Footmark no. 55 (Fig. 4B) is the deepest of the four but digit I is absent.

Claw marks are present only as thin (1–2 mm) scratches along the axes of the digit marks. They tend to be present on the digit marks although not always on all digits marks of any one footmark.

The smallest manus with three digit impressions is no. 30, with a width of 6 cm. The largest manus is no. 92, also with three digits. Its width is 11.5 cm.

Pes—Measurements of pes footmark no. 63 (Fig. 3B) are presented in Table 2. It has suffered a small amount of breakage at the tips of all digit marks, but the damage is slight and equal for all. The measurements of the damaged digit marks are presented with no corrections for breakage.

The medial and lateral side of the pes footmark can be determined by evidence of lateral skidding, and the inspection of footmarks no. 7 and no. 9a. Footmark no. 7 is a right pes print and no. 9a is a left pes print of subaqueous trackway X.

Generally digit mark III does not extend as far posteriorly as does either digit mark II or IV. Only rarely will mark III extend posteriorly beyond IV.

The pes footmarks are deeper overall than the manus footmarks and, in the pes footmarks, the deepest digit mark is III. This indicates that most of the force of locomotion passed through the hindlimb and digit III.

In six pes footmarks there are postero-medial extensions of digit mark II (Fig. 5). Footmark no. 18 (Fig. 5C) has the shortest extension; it is 3.5 cm long. The largest extension is on no. 75 (Fig. 5E); it is 8 cm long. The mean for the six footmarks is 5.5 cm with a standard deviation of 1.3 cm. Five of these footmarks are illustrated in Fig. 5. The presence of the extension does not correspond with deeper or larger prints.

TABLE 2. Pes Mark, based on no. 63 (Fig. 3B). Total length: 16 cm. Total Width: 17 cm.

Digit Mark Number	II		III		IV
Digit Mark Length	15.5 cm		13.5 cm		14.5 cm
Interdigital Distance		6.5 cm		9 cm	
Digit Mark Angle (in degrees)		0		0	

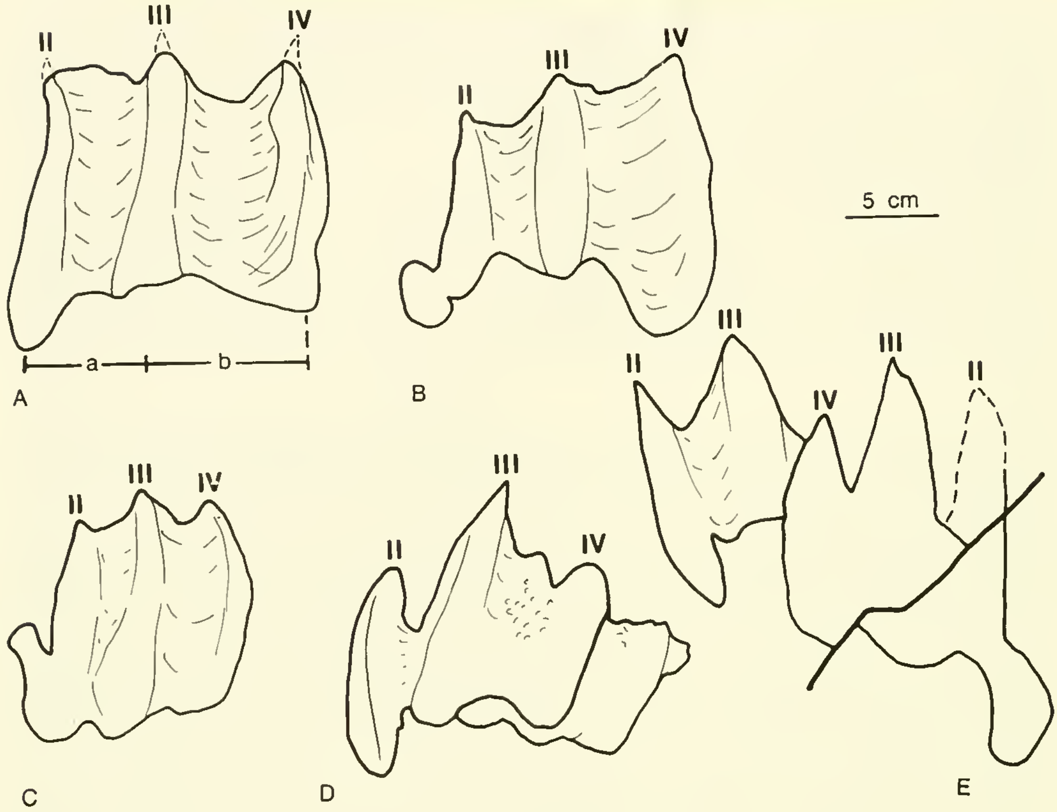

Fig. 5. Sketches of selected pedes footmarks from KUVP 5914. (A) right pes mark, no. 63 with lengths a and b; (B) right pes mark, no. 78; (C) right pes mark, no. 18; (D) right pes mark, no. 26 partially covering left pes mark, no. 27; (E) left pes mark, no. 75 partially covering right pes mark, no. 77.

The smallest pes footmark is no. 35, being 9.5 cm wide, and the largest is no. 103, being 18.5 cm wide. In 40 of the best preserved footmarks, the middle digit mark has a mean length of 13.7 cm and a standard deviation of 2.6 cm.

In a select 5 pedes footmarks, the lengths a and b were measured. Length a is the distance between the midlines of digit marks II and III. Length b is the distance between the midlines of digit marks III and IV (Fig. 5A). The length a is 6.3 cm, with a standard deviation of 1.5 cm. Length b is 7.1 cm with a standard deviation of 1.6. In a general evaluation of 26 hind foot marks which could be clearly identified as right or left, it can be determined that footmarks have a smaller length a than b.

The Subaqueous Trackways—The footmarks are difficult to assign to subaqueous trackways, especially associating manus and pedes marks (compare Figs. 2, 6). With over 100 footmarks in a small area and many footmarks without clear companion footmarks, the subaqueous trackway assignments are somewhat tenuous. The assignment of footmarks to subaqueous trackways is based on similarities of width, general form and direction.

Measurements of the subaqueous trackways are presented in Table 3. The footmarks are assigned to eight subaqueous trackways as follows with the abbreviations for right = R; left = L, manus = M, Pes = P:

Subaqueous trackway R—no. 41, LP; no. 104, LP.

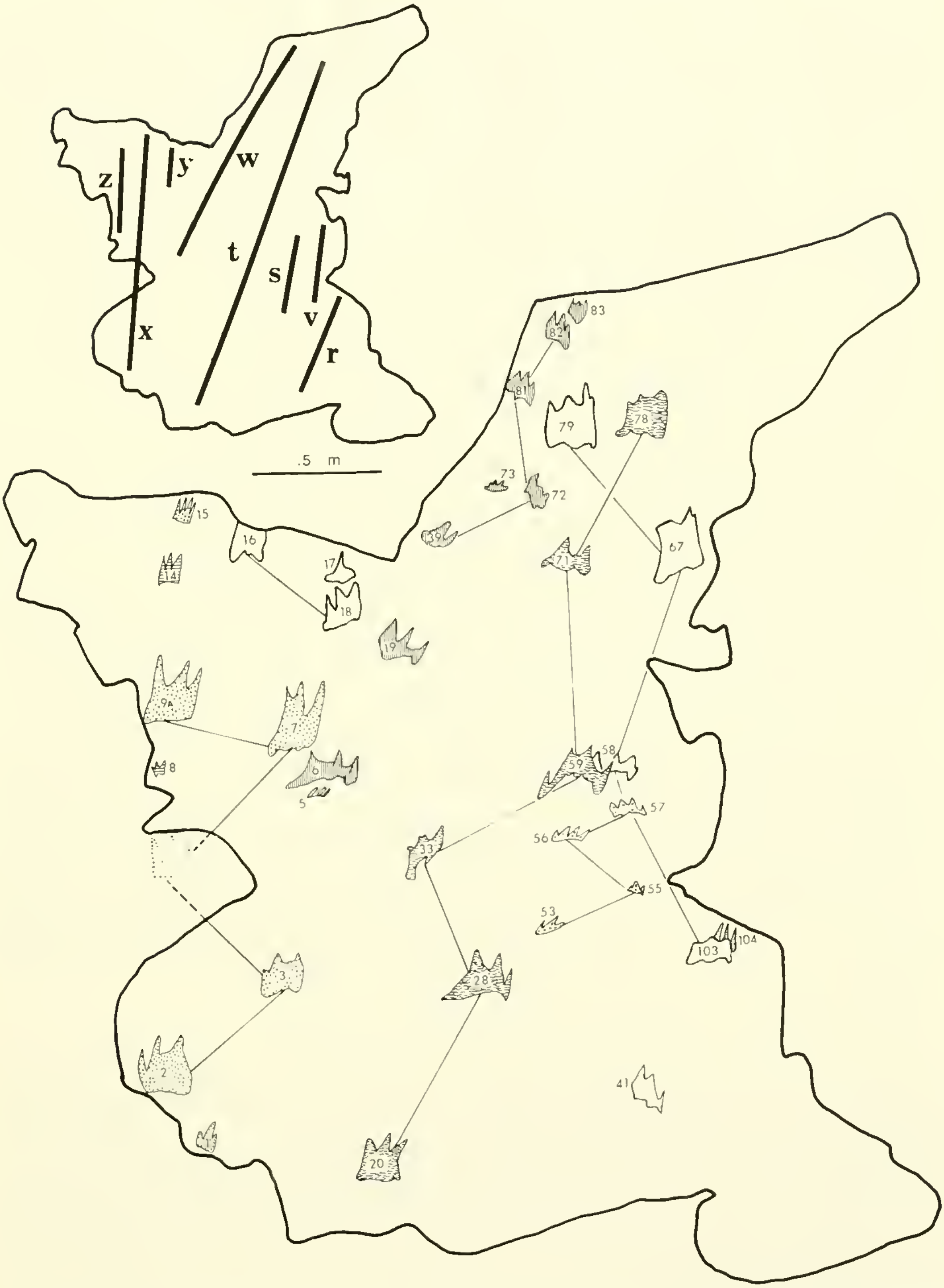

Fig. 6. The recognized subaqueous trackways on KUVP 5914. Hypothetical footmark used in pace angle measurement is indicated outside the block boundary. The insert indicates the letter assignment of each subaqueous trackway.

Subaqueous trackway S—no. 53, LM; no. 55, RM; no. 56, LM; no. 57, RM; no reliably associated pedes marks.

Subaqueous trackway T—no. 20, LP; no. 28, RP; no. 33, LP; no. 59, RP; no. 71, LP; no. 78, RP; no reliably associated manus marks.

Subaqueous trackway V—no. 103, RP; no. 58, LP; no. 67, RP; no. 79, LP;

TABLE 3. Subaqueous trackway stride and pace data.

Trackway	Stride(cm)	Pace(cm)	Pace width(cm)	Pace angulation
R	73	—	—	—
S	35	17	23	58
T	112	60	27	109
V	145	69	33	125
W	55	28	27	109
X	78	59	45	78
Y	60	30	32	80
Z	77	—	—	—

no reliably associated manus marks. These footmarks are not all well preserved and parts of the assignment may not be reliable.

Subaqueous trackway W—no. 5, LM; no. 6, LP; no. 19, LP; no. 39, LP; no. 72, RP; no. 73, R(?) M; no. 81, LP; no. 82, RP; no. 83, RM. Footmarks nos. 72, 81, and 83 indicate a turn toward the left; manus no. 83 is placed lateral to no. 82 and has sediment pushed lateral to it. Footmark no. 5 may belong to subaqueous trackway X but I consider it more probable to belong here.

Subaqueous trackway X—no. 1, LM; no. 2, LP; no. 3, RP; no. 7, RP; no. 9A, LP; no. 15, LM. The left footmark between nos. 3 and 7 is missing; it is assumed that, if the footmark block were more complete, a footmark would be present.

Subaqueous trackway Y—no. 16, LP; no. 17, R(?) M; no. 18, RP. Footmark no. 17 is an amorphous elevation in the expected position for a right manus.

Subaqueous trackway Z—no. 8, LM; no. 14, RM.

Overlapping of some footmarks occurs. This indicates a relative time sequence for the footmarks involved, as determined by the geologic law of superposition. The footmark impressed first will be partially obscured by the footmark impressed later. The latter footmark will be undisturbed. These footmarks are listed as follows, the first and second number being the partially preserved disturbed initial footmark and the later more completely preserved footmark, respectively: no. 13, no. 12; no. 32, no. 33; no. 41, no. 42; no. 48, no. 47; no. 52, no. 53; no. 58, no. 59; no. 66, no. 64; no. 67, no. 68; no. 77, no. 75; no. 89, no. 91; no. 98, no. 99; no. 104, no. 103. The second footmarks of sets nos. 78–80 and nos. 27–26 could have been produced by the same foot if the subaqueous trackwaymaker shifted its weight while using that foot. Footmark set nos. 94–95 are superimposed but it can not be determined which footmark is above or below.

The overlapping footmarks indicate overlapping subaqueous trackways. Subaqueous trackway V overlaps subaqueous trackway R (set nos. 104–103). Subaqueous trackway T overlaps subaqueous trackway V. Subaqueous trackway R is directed to the right of reference line AB (Fig. 2), subaqueous trackway V trends to the left of AB and subaqueous trackway T trends back to the right. The subaqueous trackways were produced in the order R, V and T.

The footmarks and subaqueous trackways are oriented in the direction roughly parallel to line AB (Figs. 2, 7). The footmarks range in orientation from 67 to 132 degrees. The subaqueous trackways range from 82.5 to 116.5 degrees (relative to reference line AB which was designated as 90 degrees).

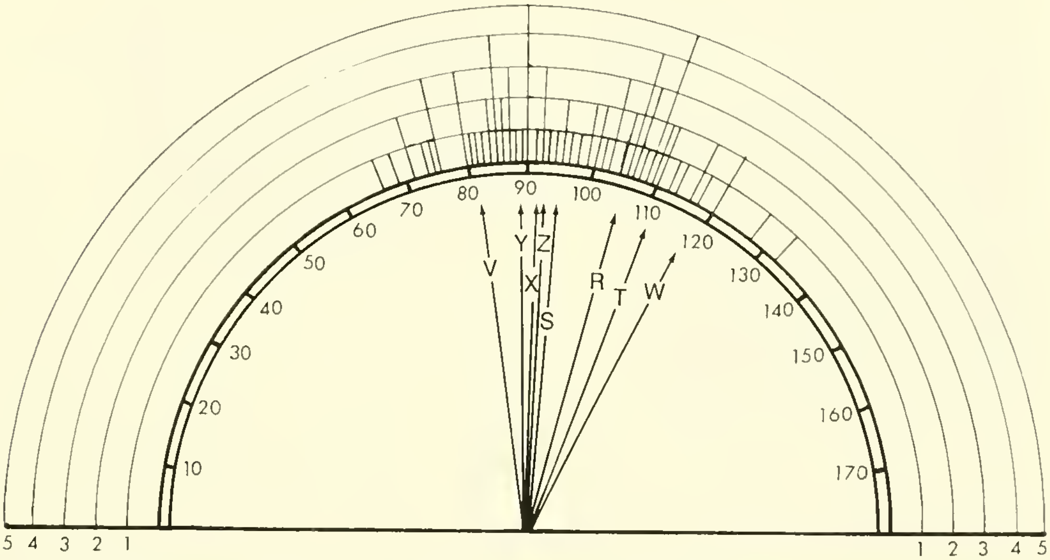

Fig. 7. Orientation of footmarks and subaqueous trackways. Subaqueous trackways are alphabetically labeled and orientation indicated within the double hemicircle. Individual footmark orientations are indicated by bars outside the double hemicircle. Footmark frequency is indicated by the length of the bar relative to scale.

INTERPRETATION

Formation—Interpreting how the footmarks were formed is basic to understanding their distribution, variability, and the kind of animal that produced them. Interpretation and even the description of these marks is difficult due to their morphological variability. The marks have the movement of the feet and the differential ability of the sediment to record these movements, superimposed on the foot morphology to create distortion and variation.

The Kansas traces were produced by a swimming animal. Subaqueous formation of these traces can best be determined by characters relating to buoyancy. The elongation of the traces, the drag marks originating from the posterior of the trace (during retraction of the limb), and the overhanging mold of the digits, all indicate special conditions of locomotion. References to fossil footmarks formed under water are uncommon, and include: Boyd and Loope (1984), tetrapod swim footmarks; Coombs (1980), a possible theropod; Gierlinski and Potemska (1987), Ellenberger (1974), Currie (1983), hadrosaur footmarks; Peabody (1948), tetrapod swim footmarks; Bird (1944), sauropod footmarks; Schmidtgen (1927), tetrapod footmarks. Further references and a discussion of recognition criteria for subaqueous traces of tetrapods are compiled in McAllister (in press).

The pes and manus marks of the Kansas subaqueous trackway are highly variable. The impression can be missing from its expected location, preserved as a thin scratch line, or present as an accurate mold of some of the digits. The subaqueous mode of formation provides a possible explanation for these phenomena. The buoyancy of the animal allows the digits to extend in an arc underneath and beyond the normal terrestrial point of gravity support. The propulsive force will be applied by the plantar surface of the digits posteriorly on a horizontal plane similar to a bulldozer.

A wide variety of traces can be produced on the substrate by a paddling animal. If the foot did not encounter much resistance from the substrate, it would continue posteriorly through the sediment following the arc described by the limb. The resultant footmark would be an elongated, striated scratch mark in the substrate, deepest in the middle. If the phalanges probe deep into the substrate, the substrate may be able to resist the force exerted and the limb will not complete the arc as described above (Fig. 8). As an example of an exceptional case, a mold of the digits was formed (Fig. 9). The digits could only point posteriorly to the travel direction if the body was buoyant and the tips of the digits did not support the body weight.

The postero-lateral extension of digit II described earlier (Figs. 5A, 5B,

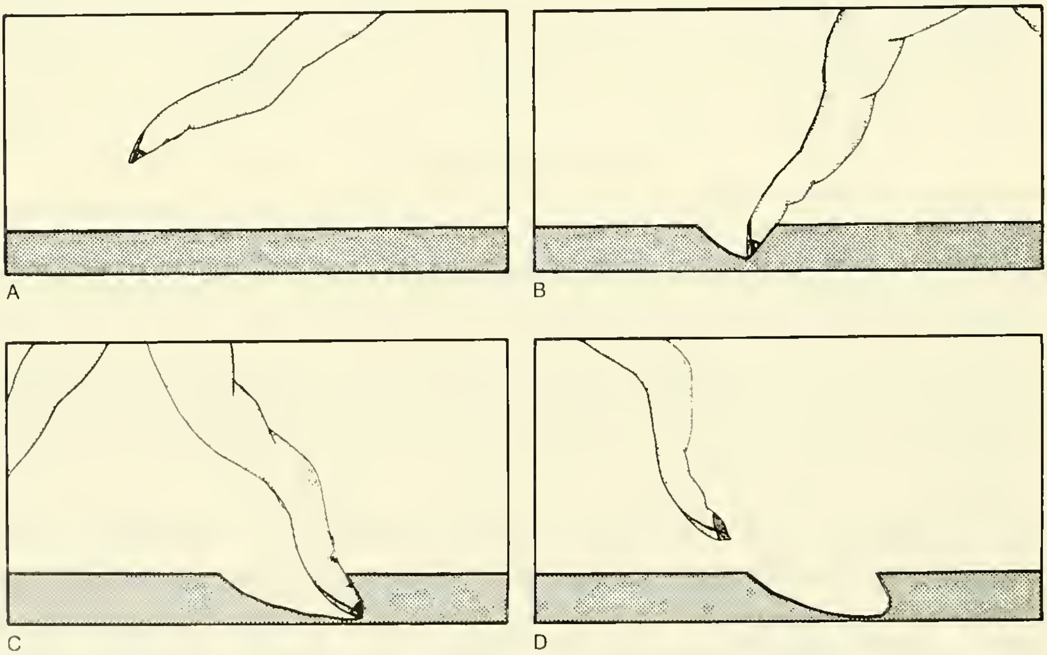

Fig. 8. Sequential movements indicating the mode of formation of the footmarks. (A) the foot of the suspended animal during initial propulsive phase; (B) digits grazing the substrate; (C) posteriorly directed digits—moving past the normal terrestrial point of gravity support; (D) culmination of footmark formation if substrate is plastic relative to force of propulsion.

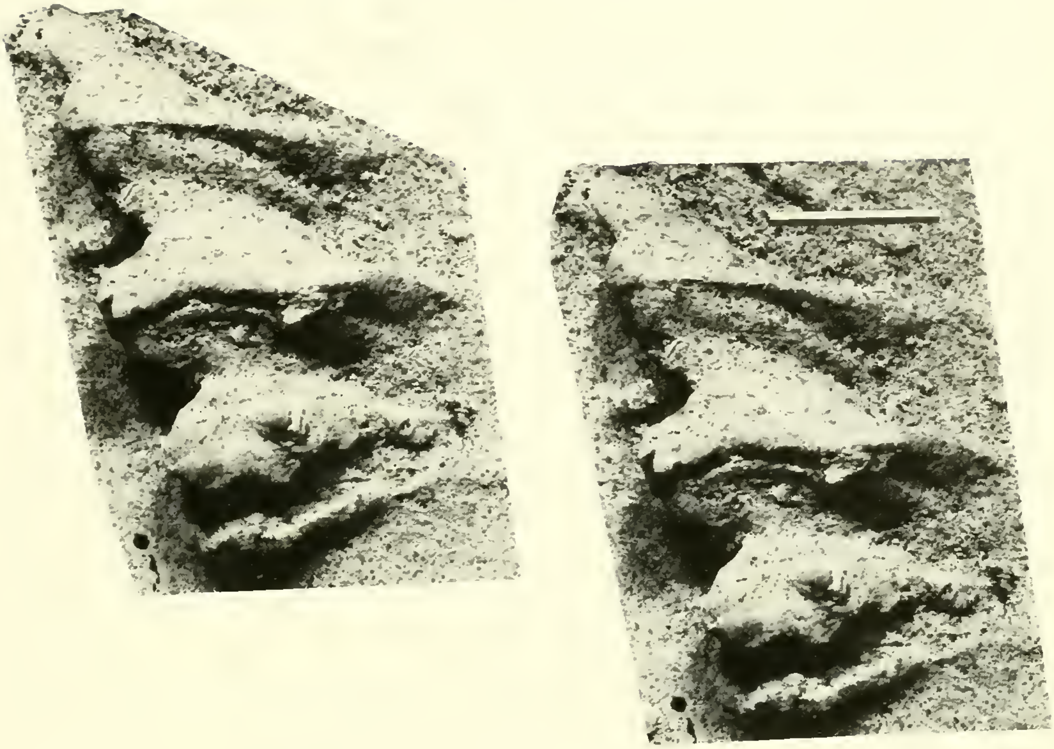

Fig. 9. Stereo photograph of right manus mark, no. 57. Scale equals 3 cm.

5D, 5E) is interpreted as a final push by the tip of digit II at the end of the propulsive phase. The continuity of the striations along the digit II mark onto these extensions confirms the continuity of digit II with the extensions and thus the common origin of both parts of the mark by digit II. The antero-lateral extension of digit II (Fig. 5C) is a drag mark of digit II during the retraction phase. For the formation of these pes marks I hypothesize that the leg was oriented outward (in abduction) and the pes was laterally-flexed during the termination of the propulsive phase. This would allow the medial digit to remain in contact with the sediment while the other digits were splayed off to the side.

Many of the footmarks have striated interdigital impressions which I consider to represent the palmar (or plantar) surfaces of the feet. The digits which formed the footmarks appear to be short, so that the metapodial-phalangeal joint would strike the substrate at a shallow depth. Alternatively, a web could have produced these impressions. I think that if interdigital webbing were present, it was not extensive because some footmarks lack interdigital impressions. Moreover, scratch and digit impressions can occur far anterior to the interdigital impressions.

This explanation of subaqueous formation explains difficulties encountered with footmarks when comparisons are made to terrestrial trackways. Footmarks may not be occurring where expected, relating individual footmarks to subaqueous trackways can be difficult, and there can be a disparity in the ratio of manus to pedes marks. A swimming animal would not necessarily touch the substrate with every propulsive stroke of each limb. This would be particularly true if the animal were swimming in water with significant wave action. There may be areas over which the animal paddled, where a footmark is expected, but no footmark is present because the foot did not reach the sediment.

The subaqueous trackway configuration can also be susceptible to greater variation compared to a terrestrial trackway. While buoyant the animal may have coasted after a propulsive stroke and not complete the locomotor cycle as quickly as when the body is not supported by water. For example, the pace angulation would be elongated in the above scenario.

The length of the forelimbs verses the hindlimbs, and the lengths of the phalanges, can affect the impression of the marks. The longer limbs and digits are more likely to impress the sediment more often and more deep. Given the same depth of water, and more numerous pes marks than manus marks, the hindlimbs of the Kansas subaqueous trackmaker are judged to have touched the substrate more often than the forelimbs. Based on this it is reasonable to infer that the subaqueous trackmaker had longer hindlimbs than forelimbs. The hindlimb left three digits marks. The middle digit mark begins a small distance anterior to the side digits and impressed the sediment deepest. The middle digit of the subaqueous trackmaker would thus be slightly longer than the other two. The manus marks are far more variable in digit mark number. The variation in length of the subaqueous trackmakers' manus digits must have been greater than the variation of the pedes digits. Manus digits I and V were shortest, digits II and IV were longer and digit III was longest, impressing the sediment deepest. In the manus marks, digit marks I and V are most commonly absent.

The direct comparison of subaqueous and terrestrial trackways would be difficult especially with increasing depth (not even considering such changes as occur in sediment competency). However, the differences and contrasts in the two types of trackways could be in themselves interesting and useful, as is later discussed under subaqueous trackmaker.

Behavior—Multiple trackways with similar orientations have been one evidence for gregarious behavior in fossil animals (Ostrom, 1972). However, Coombs (1974) suggests alternatives by which non-herding animals could create aligned trackways: these include several individuals crossing an area over several hours, a constriction in the environment, or stampeding resulting from approaching danger. Gregarious behavior for some hadrosaurs is substantiated by evidence associated with nests, taphonomy and other tracksites (Lockley et al., 1983). The Kansas footmarks are aligned in a similar direction and were produced under water where obstacles were probably not impeding their dispersal. The number of subaqueous trackways in alignment is suggestive of herding, but this is speculative. It could be possible that separate individuals were following a shoreline or currents.

The Kansas footmarks clearly indicate the ability of a large number of individuals to enter water. It is probable, due to the multiple number of subaqueous trackways, that swimming would be a normal activity for these animals.

The Subaqueous Trackmakers—Comparison of the Kansas footmarks to the known terrestrial vertebrate remains of the Kansas Dakota Formation is futile, since the only specimens, *Dakotasuchus* and *Silvisaurus*, have inadequate limb material.

In previous references (cited in the introduction) the footmarks have been considered crocodilian skid marks. I consider this unlikely due to the discrepancies in the presumed manus and pes digit formulae, the digit morphology, lack of correspondence to modern and fossil crocodylomorph trackways, and the unlikely use of limbs for paddling in a crocodylomorph-shaped animal.

The morphology (digit count and ungual phalanx shape) of the Cretaceous and modern crocodylomorphs do not fit the inferred morphology of the trackmaker. The feet of *Alligator mississippiensis* have digit formulae of five for the manus and four for the pes. All the digits have long claws. The digits, especially of the pes, are of unequal length. The expected morphology of the Kansas trackmaker would be a five digit manus, with digits of unequal length, and a pes with three subequal digits.

Crocodilian feet have remained fairly conservative in digit morphology throughout their evolution with the exception of the marine crocodiles. The Cretaceous marine forms had modified their limbs into paddles and are not likely to have created the Kansas footmarks. The feet of the Cretaceous crocodilians, the mesosuchians and eusuchians, are morphologically similar and all have a non-compatible digit count on the hind foot. Furthermore, the digit marks and especially the mold of the unguals (Fig. 9) indicate their creation by broad, possibly hoof-like, phalanges. This would be unexpected in a crocodylomorph foot.

There is no correspondence of fossil or modern trackways to the Kansas specimens. Fossil trackways assigned to the order Crocodylia are narrow; the pace angulation is between 130 and 160. The pes is tetradactyl, with digit III elongated. The tracks are plantigrade to subplantigrade (Haubold, 1971).

In terrestrial locomotion modern crocodiles do not make trackways similar to the ones described here. Cott (1961) described two customary terrestrial locomotor patterns for *Crocodilus niloticus*. One is the highwalk, in which the legs are under the body so that the venter clears the ground and the gait is trotlike. The feet are plantigrade and the tip of the tail drags (Fig. 10A). The other pattern is the bellywalk, in which the legs are held to the side of the body and the venter and tail drag on the ground. The locomotion of *Alligator mississippiensis* is described by Schaeffer (1941). It is similar to Cott's description but Schaeffer adds that in both types of walking there is an outward movement of digits III and IV in reference to the axis of the body and digits I and II. Huene (1913) described and figured walking and running trackways of *Osteolaemus tetraspis*, the West African Dwarf Crocodile, from the Frankfurt Zoological

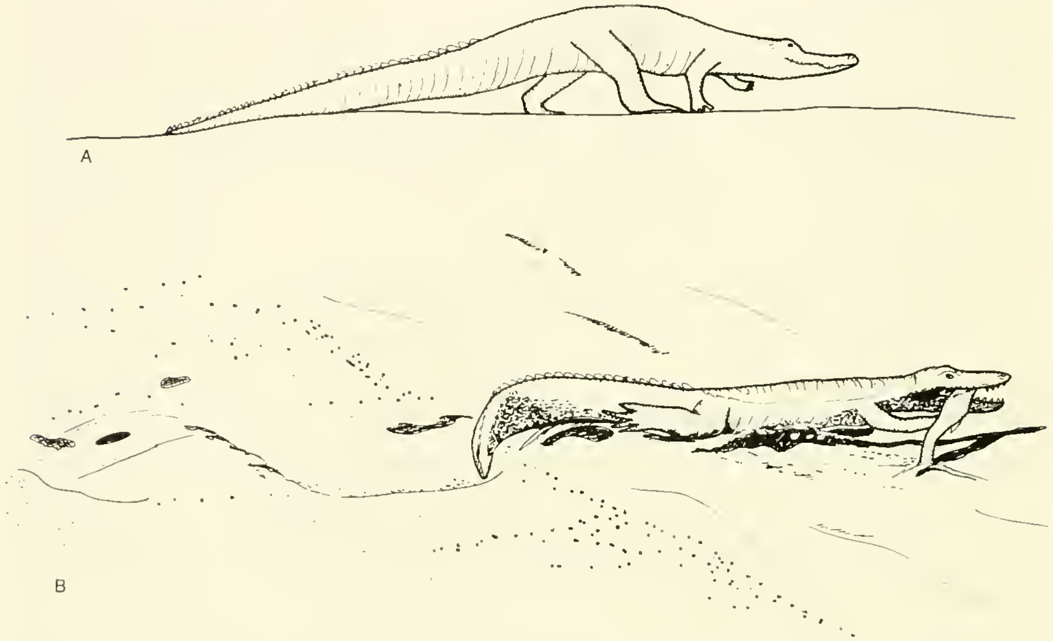

Fig. 10. Locomotion of modern crocodylomorph, based on *Crocodylus porosus*. (A) Highwalk and; (B) entrance into water from a shallow shoreline. Modified from Messel et al. (1979, Plates 3.1 and 3.24).

Gardens. The trackways were plantigrade and had venter and tail drags. A third locomotor pattern, galloping, is sometimes observed in modern crocodiles (Webb and Gans, 1982). It is usually observed in surprised individuals. The tail drags during part of the locomotor cycle creating a distinctive trackway. The Kansas trackways have no tail or belly drag, there is no outward movement of digits III and IV, the pace angulations are not within the expected crocodilian range, again in this comparison the pes digit formula is not as expected, and the digit lengths are not correct. Therefore, the Kansas subaqueous trackways cannot be considered either normal terrestrial crocodilian trackways or skidmarks produced on a mudflat as originally suggested.

The possibility that crocodylomorphs made these footmarks while partially buoyant in shallow water requires consideration of crocodilian locomotor behavior. Neill (1971, p. 388) described the use of limbs in modern crocodiles while in water:

> "The juvenile of almost any crocodilian may occasionally use the feet to make small adjustments of position in the water; but the juvenile of the African sharp-nosed crocodile ... does this more often, and more capably than any other species known to me. Both fore and hind feet are used to maintain vertical stability, to pivot abruptly in the water, and to provide braking action when the swimming reptile nears an obstruction."

I consider the minor use of the limbs in the water to be a juvenile characteristic—probably size related, or limited to adjustments of position—the limbs acting as stabilizing oars. Possibly paddling may occur while slowly moving with no discernable goal, or as a displacement behavior in larger individuals. If the Kansas trackmakers were large crocodylomorphs, moving in water over a muddy substrate, I would expect the animals to use their normal aquatic locomotion—tail propulsion with the legs against the body to increase streamlining. This is not to indicate that the limbs could not be used as braking or steering mechanism, or be used to grasp at the substrate under some circumstances, but rather that undulatory motion in a crocodylomorph will propel the animal faster than paddling and would be the preferable mode of locomotion. Observations of crocodiles (Webb and Gans, 1982; Manteer, 1940), indicate that even at the water's edge they rely mostly on lateral undulation rather than foot propelled progression. If the slope of the stream bank is steep, they belly-slide into the water. On shallow slopes they undulate their bodies, similar to swimming fish, with help from their limbs (Fig. 10B). This motion would accentuate the venter and tail drag.

The Kansas subaqueous trackways indicate a minimum of seven individuals progressing in a similar direction. I consider the probability that seven crocodylomorphs were all progressing in one direction in a paddling locomotor mode very small. Furthermore, I would expect most multiple crocodile trackwaysets to be bi-directional. Amphibious animals such as crocodiles, living along the shore would move in and out of the water. Animals which are just passing through, would tend to leave a unidirectional set of trackways.

Modern crocodylomorphs may not be an accurate analog for all aspects of fossil crocodylomorph life. Parrish (1987) analyzed the morphology of crocodylomorph limbs and determined that early crocodylomorphs were terrestrial and that the semi-aquatic condition of modern members is a secondary adaptation. Despite this I consider it is reasonable to infer that the Cretaceous crocodylomorphs would use tail swimming in the water. The zygapophyses on the vertebrae of the Kansas Cretaceous crocodylomorphs are horizontally oriented. This allows the lateral undulation necessary for tail swimming. The wide transverse processes also provide large sites for attachment of the vertebral muscles necessary for undulation. Reptiles with strongly developed flexible tails swim by lateral undulation.

The large reptiles of the Cretaceous, which would be expected to swim primarily with their feet would be turtles and dinosaurs. Turtles can easily be eliminated from consideration based on the narrow pace angles of the subaqueous trackways. No turtles of the size necessary to produce the footmarks would be able to bring their feet so close to their midline, especially without some inward inclination of the scratches.

Dinosaurs traditionally are lumped into the Saurischia (theropods and sauropods) or Ornithischia (stegosaurs, ceratopsians, ankylosaurs, and hadrosaurs). The theropods are unlikely subaqueous trackmakers because they are bipeds. The larger carnivorous dinosaurs of North America have greatly reduced forelimbs and would not likely leave a quadrupedal trackway. The subaqueous trackway described by Coombs (1980) is attributed to a theropod.

It lacks manus marks, possessed large claw marks, and the hind foot left scratch marks indicating a much larger middle digit than the side digits. The most important characters which excludes the carnivorous dinosaurs are related to the manus. The sauropods have large elephantine feet which produce round tracks. The Kansas trackmaker had five digits on the manus, and they were apparently short and hooflike, unlike either group of saurischian dinosaurs.

The other dinosaur group, the Ornithischia, provides more fodder for speculation. The North American stegosaurs were extinct before the time of the Dakota Formation and the North American ceratopsians occur later. This leaves the ankylosaurs and hadrosaurs as possible trackmakers known to be extant when the footmarks were formed.

Tracks attributed to ankylosaurs are rare and ankylosaur limb material is relatively undescribed. The ankylosaur tracks indicate a manus of a similar width to the pes and at about the same distance from the midline as the pes (Carpenter, 1984). Coombs (1971) characterizes the ankylosaur manus as follows: "The sum of the evidence for the manus is scant, but points to a formula of 2-3-3(or 4)-3-2(?), with the possibility that digit V is lost in some genera." The ankylosaur pes formula is summarized in Coombs (1986). The known pedes are either tridactyl or tetradactyl.

Mehl (1936) suggested that *Hierosaurus coleii*, from the Upper Cretaceous Niobrara Formation of Kansas, may have been fully aquatic, giving some credence to the possibility of swimming ankylosaurs. This interpretation however, is considered suspect by Eaton (1960).

Hadrosaur tracks are more abundant (providing more comparative material) and hadrosaurs reduce digits I and V in the manus and greatly reduce or eliminate them in the pes (as do ankylosaurs). Some hadrosaur manus tracks have an antero-lateral inclination of the middle digit (Lull and Wright, 1942). The posterior edges of the tracks form a postero-lateral line. The Kansas manus footmarks resemble this orientation in the manner in which the digits impress the substrate.

Neither the ankylosaurs nor the hadrosaurs can be eliminated as possible subaqueous trackmakers based on foot morphology. The Kansas footmarks do not overtly resemble either group, owing to the manner of formation, but comparisons are possible. The Kansas footmarks indicate a subaqueous trackmaker with manus digits I and V reduced, but still retaining all five digits and occasionally imprinting all digits in the sediment. Digits I and V were lost or greatly reduced in the pes as they did not impress in any of the traces. The digit count of the ankylosaurs and hadrosaurs does not eliminate these groups from consideration as possible subaqueous trackmakers. The greater relative abundance of hadrosaur tracks, the smaller size of the manus to the pes, the postero-lateral inclination of the posterior border of the forefoot imprint, the probability of gregarious behavior, and the ability to enter water (Currie, 1983) would superficially suggest hadrosaur affinities. Such evidence for ankylosaurs is unknown or based on scant evidence. Although hadrosaurs may seem more likely, the footmarks can not be assumed to be hadrosaur with any high degree of confidence at the present level of knowledge.

Identification of the subaqueous trackmaker is attempted on degrees of probability. I consider it improbable that a crocodylomorph made these footmarks because of their foot morphology and expected aquatic locomotion. Ankylosaur or hadrosaur ornithischians are at present more reasonable candidates. Each line of evidence is controvertible to some degree, but the totality of the evidence suggests ornithischian subaqueous trackmakers.

SUMMARY

Footmarks from a block of the Dakota Formation, Upper Cretaceous, are described. The manus marks exhibit up to five digits, but most commonly have three. The width of the manus marks ranges from 6–11.5 cm. The pes marks display three digits. The pes width ranges from 9.5–18.5 cm, and the interdigital distance between II and III is less than between III and IV. The pes mark is more deeply impressed than the manus, and on both manus and pes, digit III impressed deepest. The manus prints occur closer than the pes prints to the midline of the subaqueous trackway and in associated subaqueous trackways are 50–60% the width of the pes print. No belly or tail drag is present in the subparallel subaqueous trackways.

The footmarks were formed by buoyant animals on a subaqueous substrate. This mode of formation explains peculiarities of the subaqueous trackway which are irresolvable if the trackmakers are considered terrestrial. These problems include: variable impressions of the manus and pes within the subaqueous trackways; lack of footmarks where they would be expected; variable pace angulations; difficulty in associating footmarks to subaqueous trackways; and the disparity in the ratio of manus and pes marks. Subaqueous formation is indicated by such features as: elongation of the footmarks; striations which parallel movement; posterior overhangs; drag marks of the digits during retraction; and the sharp increase in depth of the footmarks corresponding to the arc of the limb during propulsion.

Designation of the subaqueous trackway as crocodilian was originally based on the co-occurrence of *Dakotasuchus* in the Kansas Dakota Formation, the unusual nature of the footmarks, and lack of information on the mode of formation of subaqueous traces. It is doubtful the footmarks are crocodilian in origin based on the following evidence: 1) the manus footmarks indicate that the phalanges are broad and short, unlike crocodilians; 2) the lengths and numbers of the digits (manus: 5, pes: 3) are not consistent with known crocodylomorph feet; 3) the subaqueous trackways are not compatible with terrestrial trackways of modern or fossil crocodylomorphs; 4) crocodylomorphs should leave tail and venter drag marks in water where their feet can touch the substrate. This is because their normal aquatic locomotion would use lateral undulations of their bodies and tails while pressing their limbs to their bodies to increase streamlining.

Although the question "What was the trackmaker?" is on the top of the list of questions most frequently asked concerning tracks, it is the most speculative one to answer. I consider the subaqueous trackmaker of these footmarks to have been ornithischian dinosaurs (ankylosaurs or hadrosaurs) based on the discernable morphological details of the feet (manus and pes digit count, shape of the ungual phalanges) and the paddling mode of aquatic propulsion.

ZUSAMMENFASSUNG

1933 wurde eine Fährtenplatte von 3,5 x 3,0 m Ausmaß mit über 106 großen Trittsiegeln aus der oberen Dakota Formation, Oberkreide, im zentralen Kansas geborgen. Die Trittsiegel bilden zumindest sieben unvollständige Fährten.

Die Färten wurden von schwimmenden Tieren auf einem Substrat unter Wasser hinterlassen. Hinweise auf eine Bildung unter Wasser sind die langgestreckten Trittsiegel und die Riefung parallel zur Bildung des hinteren Überhangs. Hinweise auf Umbiegung der Zehen und eine deutliche Zunahme der Tiefe der Trittsiegel entsprechen dem Bogen, den die Extremität während der Vorwärtsbewegung beschreibt.

Die Fährten waren ursprünglich als Krokodil-Fährten angesehen worden. Das wird hier bezweifelt, weil Krokodile ihre Extremitäten nicht zur Fortbewegung im Wasser benutzen. Außerdem stimmt die Anzahl der Zehen und der Zehengang der Fährten nicht mit der zu erwartenden Anzahl von Eindrücken und dem Gang bei den bekannten Krokodilen überein. Durch morphologische Vergleiche werden Ornithischia als mutmaßliche Erzeuger der Fährten angenommen.

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